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ALTERNATION OF GENERATIONS IN ANIMALS FROM A BOTANICAL STANDPOINT.[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXVIII.

CHARLES J. CHAMBERLAIN

(WITH TWO FIGURES)

SINCE zoologists do not recognize in animals an alternation of generations comparable with the alternation of gametophytic and sporophytic generations in plants, it may seem presumptuous for a botanist to propose any theories. Nevertheless, after hesitating for several years I have decided to publish my belief that animals exhibit an alternation of generations comparable with the alternation so well known in plants.

In short, the theory is this: the egg with the three polar bodies constitutes a generation comparable with the female gametophyte in plants; similarly, the primary spermatocyte with the four spermatozoa constitute a generation comparable with the male gametophyte in plants. All other cells of the animal constitute a generation comparable with the sporophytic generation in plants, the fertilized egg being the first cell of this series.

In support of this theory I shall present two lines of evidence: (1) the gradual reduction of the gametophyte in plants, with the constantly diminishing interval between the reduction of chromosomes and the process of fertilization; and (2) the phenomena of chromatin reduction in both animals and plants.

1. EVIDENCE FROM THE REDUCTION OF THE GAMETOPHYTE IN PLANTS.—For convenience, the female and the male gametophyte will be considered separately. Further, since dioecism in gametophytes is regarded as a more specialized condition than monoecism, and since the tendency is toward dioecism, all cases in which the gametophytes have not attained the dioecious condition may be disregarded.

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[1] Presented before Section G of the A. A. A. S., at the Philadelphia meeting, December 30, 1904.

(1) *The female gametophyte.*—In the liverworts the gametophyte is a green, independent plant. It is the conspicuous generation, the sporophyte being comparatively small and never entirely independent. Here the gametophyte generation, beginning with the spore mother-cell and extending to the fertilization of the egg, is a complex plant, of which the egg, the culmination of the gametophyte, constitutes only a very small part. In the mosses the disparity between the gametophytic and sporophytic generations is not so marked, but the gametophyte is still predominant and independent, while the sporophyte never becomes entirely independent. In the ferns the sporophyte has become the conspicuous, independent generation, and the gametophyte is much reduced. In most cases the gametophyte is still a green independent plant, although it is so small that it is likely to be overlooked by the layman. In the heterosporous forms the gametophyte is still smaller, develops little or no chlorophyll, and shows but little differentiation. Compared with the liverworts or mosses, or even with the homosporous ferns, the interval between the reduction of chromosomes and the fertilization of the egg has been immensely reduced.

In the gymnosperms the gametophyte is entirely dependent, being parasitic in the sporophyte at all stages of its development. Although there is a more or less prolonged period of nuclear division before cell walls are formed, the ancestors of these gametophytes were doubtless cellular from the beginning of their development. In *Gnetum Gnemon*, cell walls are formed only in the lower portion of the gametophyte, in the upper portion the nuclei lying free in a common layer of cytoplasm. Any one of the free nuclei of the upper portion seems capable of functioning as an egg nucleus. In other species of the same genus no walls are formed even in the lower portion, all the nuclei lying free in the general cytoplasm. In the angiosperms, both the conditions shown by the genus Gnetum are found, but reduction has proceeded much farther. A considerable tissue is formed in the lower portion of the gametophyte in Sparganium, in the grasses, and to a less extent in some Compositae and other forms; the tendency, however, is toward the free nuclear condition already reached by the latter type of Gnetum. The gametophyte of Peperomia, with its sixteen free nuclei, one of which functions as an egg nucleus, does not differ very markedly from the free nuclear type of gametophyte seen in some species of Gnetum. Four mitoses of the simultaneous type give rise to these sixteen nuclei, one of which becomes the egg nucleus. Between the reduction of chromosomes and the fertilization of the egg there are only four mitoses. In many angiosperms, as in Lilium, the interval is still shorter, the gametophyte containing only eight nuclei, resulting from three mitoses. This is the most reduced female gametophyte yet discovered in plants, and it shows only one more mitosis than does the gamete-producing generation in animals, which regularly shows two mitoses.

Up to this point I have made no mention of the tetrad of spores, a feature almost universal in plants above the thallophytes. Where the tetrad is present, the reduction of chromosomes takes place during the two mitoses by which the four spores are formed from the mother-cell. It is only in some heterosporous forms that the tetrad is incomplete or fails to appear. In such cases the reduction takes place during the first two mitoses in the mother-cells, so that whether a tetrad is formed or not, the reduction takes place during the first two mitoses in the mother-cell. To suggest that the gametophyte of the Lilium type represents a reduced tetrad might only cause confusion, and since the question does not affect essentially the theory proposed, I shall not discuss it at this time, but shall depend for comparison upon forms in which a tetrad is present. With a few well-known exceptions, one member of the tetrad develops, while the other three are evanescent and have no obvious function. It is only rarely that any nuclear division occurs in the three evanescent spores of the tetrad. In the functional spore of the tetrad three mitoses occur, giving rise to eight free nuclei, one of which becomes the nucleus of the egg.

I believe that this latter condition—the most prevalent one in angiosperms—corresponds closely with the egg and three polar bodies so characteristic of animals. In my opinion, the egg with its three polar bodies constitutes a generation directly comparable with the gametophytic generation in plants. The accompanying diagram (*fig. 1*) illustrates the comparison. Animals do not furnish any example more directly comparable with the condition shown in *D* of the diagram. In *D* the cell which we have compared with the animal egg has undergone some development so that it contains eight nuclei. This is no serious objection, however, when we remember that in the pines the cell directly homologous with the larger cell in *D* contains thousands of nuclei, and in Gnetum contains too large a number to be counted accurately, and within the angiosperms shows a series ranging from more than a hundred nuclei down to sixteen and then to eight. Comparatively few plants have been investigated, and it is not improbable that plants will yet be found which will complete the reduction series by showing only four nuclei, or only two, or even only one. The latter condition, with the megaspore functioning directly as the egg, would be illustrated by *C* of the diagram.

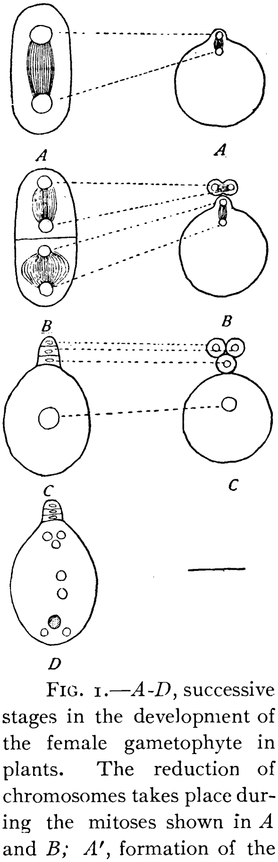

FIG. 1.—*A-D*, successive stages in the development of the female gametophyte in plants. The reduction of chromosomes takes place during the mitoses shown in *A* and *B; A′*, formation of the first polar body; *B′*, formation of second polar body and division of the first; *C′*, the egg and three polar bodies; the condition shown in *D* is not found in animals, the gamete-bearing generation in animals having become more reduced; the shaded nucleus in *D* is the egg nucleus.

To me the comparison seems so obvious that I can explain the previous absence of a theory of alternation of generations in animals only by the fact that the gamete-bearing generation is extremely reduced and is not approached by any gradual series as in plants. Had observations in plants been confined to angiosperms, there would doubtless be no theory of alternation of generations in plants.

(2) *The male gametophyte.*—It is not necessary to trace in detail the reduction of the male gametophyte. Originally a conspicuous, independent plant, it becomes reduced, loses its independence, acquires the parasitic habit, and then undergoes a progressive reduction until it becomes a simple, microscopic, parasitic structure which no one would think of homologizing with the gametophyte of a liverwort, were it not for the close series leading to the

reduced condition. In many gymnosperms the vegetative tissue has become reduced to two evanescent "prothallial" cells, and even these are lacking in most forms. In the angiosperms it is only rarely that a vestige of the vegetative tissue in the form of a prothallial cell is found.

The formation of a tetrad of spores seems to be universal. The interval between the reduction of chromosomes and the formation of the sperm is gradually reduced, until in the angiosperms there are only four mitoses in the gametophytic generation.

I believe that the condition which prevails in angiosperms is directly comparable with that found in animals. This comparison is illustrated in the accompanying diagram (*fig. 2*). Here again the plant shows a slightly more extended development, the condition shown in *E* of the diagram having no parallel in animals. But, as in the case of the female gametophyte, the objection is not serious, for the male gametophyte has been gradually reduced from a conspicuous, independent plant to a microscopic, parasitic structure with only three nuclei. It is not at all improbable that instances will yet be found in which the last two mitoses have been suppressed, the microspore functioning as a sperm. This condition could then be illustrated by *E* in the diagram.

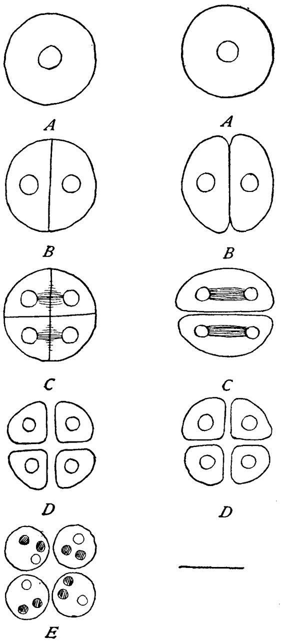

FIG. 2.—*A-E*, spermatogenesis in an angiosperm. *A*, microspore mother-cell; *B-E*, succeeding stages; the shaded nuclei in *E* represent the sperm nuclei, the unshaded nucleus being the tube nucleus; *A′*, primary spermatocyte of animals; *B′-D′*, succeeding stages; the reduction of chromosomes takes place during the mitoses giving rise to *B*, *B′* and *C*, *C′*.

The sporogenous tissue which precedes the formation of megaspore mother-cells and microscope mother-cells is comparable with the oogonia and spermatogonia of animals. Preceding the formation of megaspore mother-cells this tissue becomes much reduced in the higher plants and in many cases is altogether lacking.

2. EVIDENCE FROM THE REDUCTION OF CHROMOSOMES.—The reduction of chromosomes is a phenomenon so complex and so unique, and at the same time so essentially identical in plants and in animals, that any adequate theory must be applicable to both kingdoms. In plants the reduction always occurs during the first two divisions of the spore mother-cell, whether the plant be homosporous or heterosporous. In animals the reduction occurs during the first two divisions of the primary oocyte and primary spermatocyte. The structural character of the mitoses are too well known to need any review at this time. According to STRASBURGER[2] the reduction of chromosomes indicates a return to the more primitive gametophytic generation, and this view is quite generally accepted by botanists. I am aware that zoologists distinguish somatic and germ plasm, and that the application of this theory of alternation with its terms gametophyte and sporophyte (or rather similar terms, since "phyte" is obviously unsuitable) would cut the line of germ plasm, leaving part in one generation and part in the other. The sporogenous tissue of plants is quite analogous to the germ plasm of animals, and yet most botanists have no hesitation in assigning it to the sporophyte and in regarding the mother-cell as the first term of the gametophytic generation. The gametophytic generation—whether long as in the liverworts or short as in the angiosperms—is characterized by the reduced number of chromosomes; the sporophyte, except possibly in cases of parthenogenesis, contains double the number of chromosomes found in the gametophyte. We should recognize two generations in animals, characterized respectively by the reduced and the double number of chromosomes.

COROLLARY.

It is obvious that this theory, if well founded, affects not only the application of sexual terms in plants, but also our notions in regard to the nature of sexuality. It is hardly necessary to say that most terms relating to sexuality in plants have been borrowed from zoologists. Many botanists, especially the more rigid morphologists, have attempted to confine sexual terms to the gametophytic generation, which is spoken of as the sexual generation, while the sporophyte constitutes the asexual generation. They have ceased to speak of male trees and female trees, or male flowers and female flowers, and have ceased to regard the stamens and carpels as sexual organs.[3]

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[2] STRASBURGER, E., The periodic reduction of chromosomes in living organisms. Ann. Botany **8**:281–316. 1894.

Notions as to what constitutes a male individual or a female individual among animals, or as to what constitutes a male organ or female organ, are firmly established. If the method which the rigid botanical morphologist applies to plants should be applied to animals, the result would be interesting, for there would be no male or female individuals, nor would there be any male or female organs. All sexuality would be confined to the microscopic egg with its three polar bodies, and to the spermatocyte with its four sperms. The gametophytes of bryophytes, pteridophytes, and most gymnosperms bear well-developed archegonia, which are correctly designated sex organs, but by a gradual reduction the archegonium in the angiosperms becomes reduced to its essential structure, the egg. It is only through respect to its ancestry that this egg may be termed an organ. The antheridium is only less reduced. In animals there remain only these essential elements, which by similar courtesy may be called organs.

I prefer to apply the terminology as it is applied by zoologists, and consequently should regard dioecious sporophytes as male and female individuals. In the gametophytic generation the dioecious condition is universal in heterosporous plants. Stamens and carpels, which contain the male and female gametophytes, may be termed male and female organs as properly as may the reproductive organs of animals. It is strictly correct to speak of male and female gametophytes in plants; but in my opinion to designate the sporophyte as an asexual generation is a mistake. The sporophyte is male or female as truly as is the gametophyte; and, like the individual in animals, it is characterized by male or female reproductive organs which produce the male or female gametophytes.

I do not claim any acquaintance with zoological literature further than a reading of the latest edition of WILSON'S "The cell in development and inheritance." Were there any theories as to alternation of generations in animals, doubtless they would have been thoroughly discussed in that book.

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[3] Since any discussion of monoecism and hermaphroditism would neither reinforce nor weaken the argument these subjects are omitted altogether.

It is hardly necessary to state that the theory has no bearing whatever upon relationships or interrelationships. It merely adds another to the already long list of parallel processes, and suggests that the theory of alternation of generations in plants is applicable to animals.

THE UNIVERSITY OF CHICAGO.